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FRUITS OF THE RAIN FOREST AND TASTE PERCEPTION AS A RESULT OF EVOLUTIONARY INTERACTIONS

Claude Marcel HLADIK

INTRODUCTION

Plant and animal species that presently form the rain forest ecosystem and provide food resources to a large range of human groups are the result of long processes in which evolutionary interactions between animal and plant populations may have played an important part. During the Tertiary Era, when the continental plates were drifting apart – South and North America on one side, Africa and Eurasia on the other one – most species were quite different from those that we presently know. They differed in morphology, and – if we think of them as food – probably also in terms of composition and taste.

Rain forest fruit composition and morphology will be presented in this context of evolutionary processes. The examples are drawn from our observations in tropical Africa. Taste responses to fruits, and the generalized response to sweet sugars, also shed light on the evolutionary reason for specific food choices. This is so, despite the fact that cultural factors (as discussed in Section 6, this volume) might totally change some of the biological trends of *Homo sapiens*.

At present, fruits play an important role as food for human groups, especially in Amazonia (Clement 1993, this volume). But the indirect importance of fruit production as a resource that sustains protein production – via frugivorous animal populations – also merits close examination in terms of taste responses and fruit composition, shaped through selective pressures exerted simultaneously on animals and plants. This is emphasized in other chapters of this volume (Redford, 1993; Feer, 1993) and integrated into the socio-cultural responses of human populations (Dove, 1993).

FRUITS, SUGARS, AND COEVOLUTIONARY PROCESSES

Most fruits which are not be dispersed by wind or water flow have attractive colours and a tasty, juicy pulp containing large amounts of fructose, glucose and/or sucrose. Although these simple sugars are among the first products resulting from photosynthesis, in most plant parts, the sugars are rapidly polymerized into cellulose and/or transformed into lignin – the basic structural polymers of plants. The presence of sugars in fruit pulps, together with other nutritious components (such as fat, and sometimes protein), is a secondary process resulting from the long-lasting selective pressure of frugivorous species choosing the most nutritious fruits and dispersing their seeds.

The origin of fleshy fruits in flowering plants was imagined by Corner (1964: 223) in a fascinating description of how he sees life at the end of the Mesozoic: "When pigeons gather soon after dawn to breakfast on the red aril or mace of nutmeg, the naturalist may witness the scene that terminates nutmeg progress. Looking into the past, as nutmeg trees become pre-nutmeg and begin to coincide, perhaps, with pachycaulous ancestors of the Annonaceae, so he will see pre-pigeons and primitive birds, perhaps *Archeopteryx*, gathering at the Mesozoic break of the day. Then he may sharpen his wits on the durian and dream of pre-monkeys, pre-squirrels, pre-civet cats, pre-bears, and pre-bats gathering in clumsy confusion on low clumsy pachycaulous progenitors of durian, sterculia, bread-fruit, horse-chestnut, palm, and banana, in the beginnings of flowering forest".

This important impact of the animals eating fruits and, through seed dispersal, contributing to the success of plant species was studied by several naturalists following Darwin (Ridley, 1930; Müller, 1934). But the concept of mutualism – a phenomenon that benefits both species and makes coevolution possible – was really developed after the famous texts of Corner were published, and referred to as the "durian theory". The durian (*Durio zibethinus*) is the model of a plant species bearing large fruits and depending on large frugivorous mammals for the efficient dispersal of its seeds.

But the "durian theory" was originally applied to tropical plant species that tend to colonize open areas, outside the rain forest, requiring active transportation of large seeds. Inside the rain forest, according to Corner (1964: 219), most tree and liana species would simply shed their fruits, and the seedlings would have grown *in situ*.

Recent studies, originally inspired by these theories, have demonstrated that coevolution between plant and animal populations might indeed have originated inside rain forest areas, where species diversity is greatest, and contributed to maintaining this high biodiversity. Frugivorous birds and primates were first studied in this context (excluding invertebrate-plant interactions such as pollination and chemical defences, covered by an impressive list of books and papers). The hypothesis that fruiting species can

be selected for a fruiting period out of synchrony with the fruiting period of most other species, was presented by Snow (1966), who studied the fruiting patterns of 18 *Miconia* species in the neotropics: At present, several bird species using the various *Miconia* fruits can find their food throughout the year – taking advantage of a situation that their ancestors contributed to creating – just by feeding on fruits and dispersing seeds of plants whose reproductive cycle differ from the others. Such interactions by a group of vertebrates with several plants used as a "fruiting environment" (Herrera, 1986) are now referred to as "diffuse coevolution".

Apes and monkeys also played, and still play, a similar role as forest "gardeners", selecting the varieties of plants that bear the best fruits and contributing to the success of "good genes". The hypothesis that tropical forest regeneration was impossible in the absence of the primate fauna was tested after we had verified that intestinal transit was harmless or beneficial for most seeds (Hladik and Hladik, 1967). Comparing African and neotropical forests, we calculated the "dispersal seed flow" for trees and lianas. In a neotropical forest, the annual flow is higher than 100 000 seeds per hectare. The distance of dispersal is longer than one kilometre for most of the species whose fruits are eaten by four sympatric species of primates, as determined by the quantities actually ingested, and the distance travelled by the animals before dropping the seeds in their faeces (Hladik and Hladik, 1969). For several tree species, the dispersal activity of primates is complemented by that of frugivorous birds and bats, competing, in some cases, for the same fruit species. Together, they contribute to what has been called the "seed rain" which makes a fresh stock of seeds permanently available in the soil for regeneration. Charles-Dominique (1986) observed this phenomenom in the forest of French Guiana.

In short, the genes of plants bearing the largest and sweetest fruits would be efficiently duplicated as a result of food choices of primates and other vertebrates searching for pulps and arils with high sugar (and/or fat and protein) content. Like numerous other cases in which selective factors seem to operate, only indirect pieces of evidence support the hypothesis, but they are clear and convincing.

For instance, the analysis of fruit pulps from neotropical forest (C.M. Hladik *et al.*, 1971) has shown that fruits having the highest sugar content in the soluble fraction (mostly simple sugars that can be tasted by primates) are those of plant species that are most frequently used and dispersed, especially by *Cebus capucinus*, which takes pieces of almost any plant part found along its way and actually tastes it. The obvious result is that the seeds of plants with the sweetest fruits are dispersed in largest quantities. The maintenance or increase of plant populations through the seedling survival of such animal dispersed plant species has been emphasized in a study comparing the efficiency of various types of seed dispersal (A. Hladik and Miquel, 1990).

As a result, the sugar content of rain forest fruits is frequently as high as that of cultivated fruit species that humans have been empirically (and more recently, scientifically) selecting for sweetness and other qualities. Examples are presented in Table 7.1, including species from the Gabon rain forest, where studies of biodiversity, forest regeneration and dynamics were conducted to complement a survey of one of the most efficient seed dispersers, the chimpanzee (C.M. Hladik, 1973).

In this table, one notices among the Anacardiaceae (a family including mangoes, whose cultivated varieties contain 20% of sugar by fresh weight; Anon., 1967), the extremely high sugar content of *Trichoscypha* sp. (the "jungle grape") and of *Antrocaryon klaineanum*, both fruits being collected in forest to be sold in African local markets. Among the Burseraceae, the two *Santiria* sp. (top of the list) do require further botanical description if they are to be included in the Flora of Gabon. In fact, these two species (respectively noted I and II) share several morphological characters, but have different phenological cycles and fruit compositions. The significance of such "sibling species" was discussed by A. Hladik and N. Hallé (1979), with reference to recent species differentiation following selective pressure exerted by frugivorous seed dispersers. The flesh of the fruit of one of them (sp. I), with sugar composition 3/4 of the dry matter, is almost jam!

Of equally great interest is the fraction of fruit that is not carbohydrate. For instance, in the genus *Dacryodes* (Burseraceae), one species, *D. klaineana*, has a sugary pulp, whereas *D. buttneri* and *D. edulis* have a high fat content (neither of these two species are included in Table 7.1 because their sugar content is very low). Indeed, together with sugar, fat is important to make a "high-energy food package" of sufficiently small size to be swallowed by most potential seed dispersing species (see comments in Chapter 2, this volume). Other species at the bottom of the list have fruits with a low sugar content, and play an obvious ecological role in balancing the diet of vertebrate populations. The last one, *Anonidium mannii*, is very rich in protein (12% dry matter – which is exceptional for a fruit pulp).

This large fruit of the Annonaceae family, weighing about 5 kg, and hanging directly on the tree trunk (cauliflory), recalls some aspects of the durian fruit and leads us back to Corner's theory: such a fruit pulp would allow large vertebrates (especially primates) to obtain a balanced diet. In turn, the plant would benefit from efficient dispersal of its large seeds, especially when the animal carries the fruit to eat it in a safe place.

A single fruit of *Anonidium mannii* is sufficient to make a nutritious snack for a group of Pygmies during a collective hunting party. It can also be brought back to the village, and the Ngbaka of the Central African Republic eat the pulp after sweetening it with sugar. This might mean that evolutionary forces could still "improve" fruit composition, and there is no reason to doubt that these selective pressures are still acting among rain forest species.

Table 7.1 Composition of fruits of Gabon forest species, listed in order of decreasing sugar content. Using two different techniques[1], the sugar content was calculated as a percentage of the dry matter (in parentheses, total percentage of simple sugars including fructose, glucose and sucrose)

Species (herbarium ref. and FAMILY)	Water content (%)	Percent dry matter			
		Hydrolysable sugars		Alcohol soluble fraction	
Santiria sp. *I (AH 1424 - BURSERACEAE)*	87			76	(74)
Hemandradenia mannii (CONNARACEAE)	81			87	(54)
Salacia pierrei (HIPPOCRATEACEAE)	84			83	(52)
Santiria sp. *II (AH 2469 - BURSERACEAE)*	88			87	(49)
Dacryodes klaineana (BURSERACEAE)	90			88	(47)
Cissus dinklagei (VITACEAE)	85			80	(43)
Trichoscypha sp. *(AH 1946 - ANACARDIACEAE)*	86			85	(43)
Sarcophrynium schweinfurthianum (MARANTACEAE)	62	62			
Dialium sp. *(AH 2732 - CAESALPINIACEAE)*	35	55			
Gambeya beguei (SAPOTACEAE)	58			52	(46)
Irvingia gabonensis (IRVINGIACEAE)	89	52			
Pancovia pedicellaris (SAPINDACEAE)	83	50	(45)		
Antrocaryon klaineanum (ANACARDIACEAE)	81	45	(40)		
Pachypodanthium barteri (ANNONACEAE)	92			47	(28)
Detarium macrocarpum (CAESALPINIACEAE)	69	55	(37)		
Hugonia spicata (LINACEAE)	73	47	(33)		
Swartzia fistuloides (CAESALPINIACEAE)	37	47	(25)		
Nauclea diderrichii (RUBIACEAE)	77	47			
Duboscia macrocarpa (TILIACAE)	68	45			
Vitex fosteri (VERBENACEAE)	85	43	(32)		
Polyalthia suaveolens (ANNONACEAE)	67	41	(33)		
Uapaca paludosa (EUPHORBIACEAE)	50	33	(31)		
Staudtia gabonensis (MYRISTICACEAE)	65	33	(26)		
Parinari excelsa (CHRYSOBALANACEAE)	79	27	(16)		
Gambeya lacourtiana (SAPOTACEAE)	71	21	(13)		
Uapaca heudelotii (EUPHORBIACEAE)	84	20	(4)		
Anonidium mannii (ANNONACEAE)	85	20	(4)		

[1] This study of fruit pulp composition was conducted with two different techniques:

(1) In order to determine the content of short-chain sugars in the liquid pulp of the richest fruits, the pulp was precipitated in boiling alcohol. The alcohol soluble fraction containing the smallest molecules (most of them detected by the vertebrate taste receptor) is of paramount importance in taste discrimination and food choice.

(2) In most instances, fruits and other potential foods were analysed after desiccation of the sample, and part of the carbohydrates were detected as sugars after a weak-acid hydrolysis. This permits an assessment of the nutritional value, because the hydrolysis approximates the activity of digestive enzymes and sorts out what is digestible among carbohydrates, especially starch. In this case, the percentages of soluble sugars related to dry matter (in parentheses in Table 7.1) are indicated for comparison with the value found by the other technique (Source: Hladik *et al.*, 1971).

SUGAR MIMICS AND TASTE PERCEPTION

Plant species, competing for an efficient seed dispersal system, are faced with the necessity for plant eaters to obtain sufficient energy. In the Gabon rain forest, studies on vertebrate populations (Gautier-Hion, 1990) show that different guilds of seed dispersers are using particular fruit types containing various amounts of fructose, glucose and sucrose. The normal tendency of the ecosystem over evolutionary time is diversification of plant species (including different production cycles) and increasing sugar production in fruits.

But this requires a high energy input from plant species, and what we have called "biochemical mimicry" (Hladik and Hladik, 1988) is also likely to occur. Biochemical mimicry in plants can be compared to Batesian mimicry in animals: one species which, by chance, tends to look like another species (the "model") might benefit from its appearance. But as for an edible butterfly looking like a wasp (avoided by predators), the genetic character might be retained only if the target species is present in the environment.

For a plant, the target to be imitated can be any other species producing sweet fruits, if the plant can produce a chemical looking like a sugar but needing less energy for production. "Looking like sugar" must be understood in terms of taste response of the gustatory system of the animal dispersing seeds – for instance primates. Although there are differences among primate species (Simmen, 1992) and among human populations (Faurion, 1987) in the ability to discriminate sugars, the positive response associated with sweetness is generally a specific adaptation to find and utilize energy-rich foods (Le Magnen, 1963). But it was recently demonstrated that several types of chemical such as saccharin, dulcin, aspartam, etc. can also elicit a sweet taste response on the primate taste bud (Van der Wel *et al.*, 1989) which can be considered as an intermediate target for sugar mimicry.

Indeed, some non-sugar plant products have also been found that elicit a sweet taste response of the gustatory system of primates. They recently attracted the attention of biochemists (Langley-Danysz, 1987) for their potential use as low-calorie natural sweeteners, and of physiologists (Hellekant *et al.*, 1981) because they might enable the investigation of how sweet substances interact with protein taste bud cells. If the present ecological role of these sweet substances among rain forest plant species is to be interpreted in terms of biochemical mimicry, further understanding of the coevolutionary processes discussed in the preceding pages is required.

For instance, the red berries of a Menispermaceae, *Dioscoreophyllum cumminsii,* that have an extremely sweet taste do not contain sugar, but a protein ("monellin") which is 100 000 times sweeter than sucrose at the same molar concentration. Accordingly, the energy necessary to grow such fruits is significantly lower than that required to grow fruits containing

sugar. Another fruit of the Marantaceae family, *Thaumatococcus daniellii*, is also known for the strong sweet taste of its yellow aril, due to small amounts of another protein called "thaumatin". Since all African primate species that have been tested can perceive the sweet taste of monellin and thaumatin (Glaser *et al.*, 1978), they are likely to eat the fruit and act as efficient seed dispersers. The evolutionary interactions linking these plants to the primate species – and ultimately allowing the emergence of low-energy-demanding sugar mimics among other plants bearing fruits with "true sugar" – is presently the best explanation for both the presence of these substances and the differences in perception of primate species elicited by them.

In fact, the results of tests conducted on different primate species surprised the first investigators: Whereas African primates react positively towards solutions of monellin and thaumatin, the New World primates (except for a few species which showed a weak reaction to monellin) do not differentiate these solutions from plain water (Hellekant *et al.*, 1981). This quasi-absence of reaction was interpreted in terms of primate phylogeny: Continental drift separated African and American primates before the taste buds of African primates (Catarrhini sub-Order, including humans) became differentiated from those of the original stock of American primates (Platyrrhini sub-Order). This interpretation is quite compatible with sugar mimicry. But, in order to understand why the New World primates are not able to taste these sugar mimics, we have to bear in mind that African plant species evolved in relation to what the primates of the *African* forest can actually perceive as sweet. If sugar mimics also exist in the New World forests (this is purely hypothetical), the coevolutionary process would have occurred according to the taste ability of the Platyrrhini. In this case, people (as Catarrhini), would probably find them tasteless.

Indeed, sugar mimicry arose in different plant families, and, at least in Africa, it is not rare. In addition to the Menispermaceae and Marantaceae, we have recently found another sweet substance in the fruit of *Pentadiplandra brazzeana* (Pentadiplandraceae), a protein we named "pentadin" (Van der Wel *et al.*, 1989), which is still under investigation.

Most of these sweet fruits are known by local people and sometimes used for sweetening other foods (FAO, 1989). In the Central African Republic and south Cameroon, Aka and Baka Pygmy children are fond of the strong sweetness of *Dioscoreophyllum cumminsii* fruits, in spite of their aftertaste that may last several minutes. The fruit of *Pentadiplandra brazzeana* is known in Gabon, with "l'oubli" ("forgetting") as a French name; people say that children are so fond of the red pulp of this fruit that they may forget their mother while looking for them. In Zaire, the Oto and Twa children also crave for these fruits (H. Pagezy, pers. comm.).

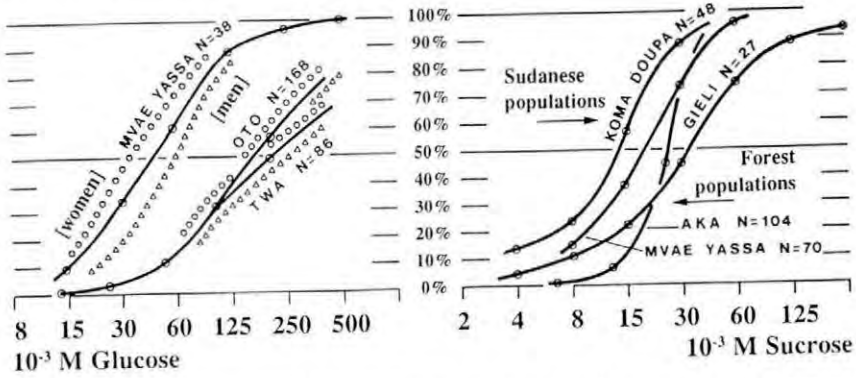
Nevertheless, the preference for fruits with high sugar content remains an expression of the fundamental quest by forest people for energy-rich food.

SUGAR PERCEPTION IN FOREST POPULATIONS

During food surveys conducted in Cameroon (Koppert *et al.*, 1993, this volume) and the Central African Republic, we determined the taste thresholds for purified natural products. Some of the results illustrated in Figure 7.1 show that differences in taste thresholds between various populations may vary according to different types of chemical tested. For instance, the difference between forest populations and people living outside of the rain forest is wide for glucose, narrower, but still significant ($p < 0.05$) for sucrose, whereas no significant difference was found for fructose. This means that any "sweetness equivalent", experimentally determined (for instance the concentration of glucose required to elicit the same taste response as that of a standard sucrose concentration), may be solely valid for the population tested. Most of these equivalents are presently calculated for Europeans and North Americans (for instance: if sucrose = 1, then fructose = 1.73 and glucose = 0.74; Le Magnen, 1963). In fact, a "perception spectrum" has to be determined for each population separately.

Furthermore, the feminine and masculine sub-populations may also present different taste sensitivities. This is illustrated in Figure 7.1 for non-Pygmy

Figure 7.1 Taste thresholds for glucose and sucrose in different populations living inside and outside the African rain forest. Each of the curves shows, for a given population (or a group of populations), the cumulative percentages of people able to recognize the taste of a solution at a given concentration, during standardized tests[1]. Aka and Kola (Gieli) Pygmies of the Central African Republic, and the Mvae and Yassa of south Cameroon – all forest populations – have a significantly higher threshold than the populations of north Cameroon (Koma and Doupa). The difference between men and women in glucose taste sensitivity, is not significant for Pygmies but significant ($p < 0.05$) for Mvae and Yassa.



[1] The tests were conducted by presenting at random, glucose, sucrose, fructose, sodium chloride, organic acids, and bitter substances, from the weakest solution in order of increasing concentration (10^{-3} M sucrose = 0.34 g l^{-1}). Statistical tests (χ^2) allow determination of significant differences between populations (Hladik *et al.*, 1986).

forest populations among which women have a significantly higher taste sensitivity for glucose than men. Such differences, also observed in other populations and for other products (sodium chloride and organic acids), have been discussed with respect to the cultural context that may imply taste training for women (Hladik *et al.*, 1986; Robbe and Hladik, 1988).

The major difference observed in Africa is a higher taste sensitivity for sugars among the people living outside the rain forest as compared to forest peoples. All Pygmy populations tested have a high threshold (that is a low sensitivity). One may wonder why Pygmies are so highly motivated to struggle with wild bees in order to collect honey from hollow tree trunks (Bahuchet, 1985) and to climb trees to collect sweet fruits.

The evolutionary interactions presented in the preceding pages explain why, in the "sweet biochemical environment"of the forest – where the sugar concentration in fruit pulps is 10 to 50 times the Pygmy taste threshold – there is no reason for a high taste sensitivity to evolve. Conversely, for *other populations* living outside the rain forest, where biodiversity and thus competition between fruiting species is not as high (and sweet fruits rather scarce), a slightly higher taste sensitivity would be adaptive to foods lower in sugar. Hence the differences between populations presently observed. But the time-scale necessary for the emergence of such differences is obviously very short (a few thousand years) when compared to the millions of years that allowed the emergence of new species.

Compared to these long-term and short-term biological changes, cultural adaptations have to be considered on another extremely short time-scale. Nevertheless, we should always bear in mind that the cultural traits that make human food choices vary so widely between different groups – as illustrated in several other chapters of this volume – were integrated into the biological framework resulting from long-term evolutionary interactions.

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